New data on *Theba subdentata helicella* (Wood, 1828) (Gastropoda, Helicidae) in Almería (SE Spain)

Nuevos datos sobre *Theba subdentata helicella* (Wood, 1828) (Gastropoda, Helicidae) en Almería (SE España)

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ABSTRACT

The distribution of *Theba subdentata helicella* (Wood, 1828) in the Eastern part of the Almería Bay is studied. This paper confirms the existence of rich populations of *T. s. helicella* inhabiting the lowlands close to the sea, never reaching the surrounding mountains. Information on the habitat, shell and genital system variability is provided.

The shells show a characteristically depressed and sharply keeled shape, and are usually white or with a light brown to orange spiral band near the carina in all populations except in Amoladeras watercourse (inside the Cabo de Gata-Níjar Natural Park). In this locality there is a gradation from the typical form to almost globular specimens with a very slight keel, nearly wanting, only visible on the last half of the body whorl near the aperture, similar to *T. s. dehnei* (Rossmässler, 1846) from Morocco. These shells show basal bands or blotches that remind those of *Theba pisana pisana* (O.F. Müller, 1774) or *T. s. dehnei*.

The genital system of the Amoladeras population is compared with those described for *T. s. helicella* y *T. s. dehnei* from Morocco, confirming that it shares more characters with the first subespecies. A discriminant function analysis of shells characters measurements of two populations of *T. s. helicella* and *T. p. pisana* allowed to discard the hypotesis of an hybrid origin of the globose specimens.

Data on the presence and habitat of other gastropod species living with *T. s. helicella* in the study area are provided.

RESUMEN

Se estudia la distribución de *Theba subdentata helicella* (Wood, 1828) en la mitad oriental de la bahía de Almería, su principal área de presencia en Europa, confirmando la existencia de poblaciones abundantes y aportando información sobre el hábitat, la variabilidad de la concha, y su aparato genital. Esta subespecie se distribuye por los terrenos llanos próximos al mar sin llegar a ocupar las montañas próximas.

En general, en todo el área de estudio las conchas de *T. s. helicella* corresponden a la forma típica aquillada, aplanada y generalmente de color blanco o con una banda espiral dorsal oscura, mientras que en la población de Amoladeras (dentro del Parque Natural de Cabo de Gata-Níjar), existe una gradación desde la forma típica a otra globosa y ligeramente aquillada o sin quilla en la vuelta del cuerpo, similar a la de *Theba subdentata dehnei* (Rossmässler, 1846) de Marruecos. Ésta presenta distintos patrones de pigmentación, con varias bandas y manchas, que recuerdan a los de *Theba pisana pisana* (O.F. Müller, 1774) o *T. s. dehnei*.

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El sistema genital de la población de Amoladeras se compara con los descritos para *T. s. helicella* y *T. s. dehnei* de Marruecos, confirmando que comparte más caracteres con los de la primera subespecie. Un análisis discriminante de las medidas de la concha de dos poblaciones de *T. s. helicella* y las de *T. p. pisana* permite rechazar la hipótesis de hibridación como origen de las formas globosas.
Se incluyen datos de la presencia y hábitat de las especies de gasterópodos terrestres halladas en el área de estudio y que viven en simpatría con *T. s. helicella*.

KEY WORDS: *Theba subdentata helicella,* Helicidae, distribution, taxonomy, variability, faunistics, Cabo de Gata, Almería, Spain.
PALABRAS CLAVE: *Theba subdentata helicella,* Helicidae, distribución, taxonomía, variabilidad, faunística, Cabo de Gata, Almería, España.

INTRODUCTION

Theba subdentata (Férussac, 1821) is a polytypic species with its main range in Western Morocco. According to GITTENBERGER AND RIPKEN (1987), it is an extremely variable species that "...has been rather arbitrarily subdivided into five subspecies: *T. s. subdentata* (Férussac, 1821), *T. s. helicella* (Wood, 1828), *T. s. dehnei* (Rossmässler, 1846), *T. s. meridionalis* (Sacchi, 1955) and *T. s. legionaria* (Sacchi, 1955)". Gradual variation among subspecies has been described for several shell characters, apparently related to habitat variation. *Theba s. helicella* lives in sand-dunes along the Moroccan coast in the northern part of its range. It is known from c. 30 km S of Safi extending southward to c. 35 km NW of Agadir (GITTENBERGER AND RIPKEN, 1987; GITTENBERGER, RIPKEN AND BUENO, 1992). *Theba s. helicella* has a characteristically depressed and sharply keeled shell, although this character varies gradually from north to south, shifting to more rounded in southern specimens, such as *T. s. dehnei*, a subspecies that inhabits rocky areas. Intermediate forms have been found in places where sand-dunes and rocky areas converge (GITTENBERGER AND RIPKEN, 1987).

GITTENBERGER AND RIPKEN (1987) cited a sample of *T. s. helicella* in the RMNH Leiden (Altimira collection), believed to originate from El Alquián, Almería (Spain). After "...trying in vain to confirm this record", the authors concluded that this population had probably been introduced in Spain and had eventually become extinct. After that, PUENTE, ALTONAGA, UNAMUNO AND PRIETO (1994) found three specimens (one adult, one sub-adult and one juvenile) of this subspecies at Cerrillos, 35 km west of El Alquián, and provided a drawing of the adult genital system. These specimens confirmed the presence of *T. s. helicella* in Europe. The first record of a live population of *T. s. helicella* in El Alquián was reported by MORENO AND RAMOS (2000), who stated that the Eastern limit of distribution is located inside the protected area of the Cabo de Gata-Níjar Natural Park.

After that, GÓMEZ, MORENO, ROLÁN, ARAUJO AND ALVAREZ (2001) proposed the inclusion of this taxon in the National Red List of Endangered Species (Catálogo Nacional de Especies Amenazadas) as "Vulnerable". Later, MENEZ (2006) provided some data on the habitat and density of the population of *T. s. helicella* at Retamar and El Alquián (Almería).

In this paper we confirm the existence of a numerous and healthy population in El Alquián and extend its previously known distribution to further areas of Almería Province. Shell characters and character variation throughout its distribution range in the study area are described and compared with those of the sympatric and congeneric taxon

Theba pisana pisana (O.F. Müller, 1774). For the first time, the characters of the genital system and their variations are described for the population of *T. s. helicella* in El Alquián. They are compared with the Moroccan populations of *T. s. helicella* and with the closely related subspecies *T. s. dehnei*, from data published in the literature (Hesse, 1915). Ecological data are also provided with considerations of the conservation status of the subspecies in Spain. Other species of terrestrial molluscs are also cited for the study area.

MATERIALS AND METHODS

We explored the entire Eastern zone of the Almería Bay, between the Almería airport (El Alquián), and Cabo de Gata mountains (excluded). The first live population of *T. s. helicella* was found in March 1994 in El Alquián. After that, the area was explored looking for *T. s. helicella* in order to confirm the limits of its distribution area. All the different gastropod species observed were collected. The abundance of all species was estimated from the number of specimens and/or fresh shells collected or observed, during the sampling effort, about 10-15 minutes, in each locality.

The sampling localities (Table I, Fig. 1) were all in Almería province, and are listed from West to East in Table I. UTM coordinates, sampling dates, a brief description of the substratum and dominant vegetation are provided for each locality. UTM coordinates were obtained from the official Army Geographical Service map (1:50.000 series).

The littoral of the study area is characterized by sandy beaches, dunes, "ramblas" (seasonal watercourses), a vegetation comprised of mostly African species (as *Ziziphus lotus*), and a semiarid climate, with only 200 mm of rainfall each year. Upstream, from El Barranquete (Rambla del Hacho, on its right bank), there are rocky areas with conglomerates at 60 m altitude above sea level (the highest point among the studied localities). From here begins the Serrata de Níjar, the volcanic mountains that lie before the Cabo de Gata mountains, excluded in the present study.

Shell measurements were obtained with a calliper or using the micrometric ocular of the stereomicroscope. For the estimation of the number of shell whorls the method of Verduin (1976) was used. Shells were first cleaned with ultrasound and the periostracum was removed by immersion in a 5% solution of sodium hypochlorite. With an Environmental Scanning Electron Microscope (ESEM) Philips Quanta 200 SEM in low vacuum mode, shells were studied without gold coating and photomicrographs were taken. For anatomical studies, animals were first immersed in water until death and then preserved in 70% ethanol. Dissections were made in water on cork or on a Petri dish with a black layer of paraffin, wax and coal (Davis, 1967). A Stemi SV8 Zeiss stereomicroscope was used for observations and measurements. Genital photographs were taken with an Olympus SZH10 stereomicroscope. Anatomical illustrations were based on camera-lucida drawings.

Abbreviations used in text, tables and figures are:

Shell measurements. AH: aperture height, AW: aperture width (maximum diameter of the aperture), NSW: number of shell whorls, SH: shell height, SW: shell width, UD: umbilicus diameter, WBW: width of the body whorl. Measured shells and measurements are in Table III.

Genital system. ag: albumen gland, bc: bursa copulatrix, dd: distal part of the bursa copulatrix duct, di: diverticulum, ds: dart sac, e: epiphallus (from penis retractor muscle to vas deferens), f: flagellum, fod: free oviduct, hd: hermaphrodite duct, hg: hermaphrodite gland, mg: mucosae glands, p: penis, pd: proximal part of the bursa copulatrix duct, pp: penis papilla, prm: penis retractor muscle, rp: radial pleats, v: vagina, vd: vas deferens, vs: vesicula seminalis, Measured organs and measurements are in Table IV.

Collectors. Sampling and field observations were carried out by D. Moreno and N. Martín between 1994 and 2006.

Table I. Sampling localities in the study area, from west to east, with UTM coordinates, collection dates, a brief description of the substratum and dominant vegetation. All localities in Almería Province. Localities 7, 8, 10-23 and 25-28 are inside the Cabo de Gata-Níjar Natural Park. "Rambla" = seasonal watercourse.

Nº	Localities	UTM	Collection dates
1	Torre del Perdigal, El Alquián	30SWF563777	8-III-1997, 10-III-1997
2	Playa de El Alquián, fishing boats area	30SWF563777	8-III-1997, 10-III-1997
3	Dunes between El Alquián-Casa Fuerte	30SWF585775	8-III-1997
4	Casa Fuerte, El Alquián	30SWF602771	31-III-1994, 15-I-1995, 10-III-1996, 8-III-1997, 1-V-2002, 20-VI-2002
5	Cortijo el Pino, El Toyo	30SWF607783	23-XI-2000
6	Urbanización de Retamar	30SWF616785	15-I-1995
7	Rambla del Agua, Retamar	30SWF620763	15-I-1995, 5-IX-1997, 12-IX-1997
8	Forest trail to Torregarcía, western area	30SWF633761	15-I-1995, 8-III-1997, 5-V-2006
9	Cortijo del Retamar	30SWF633789	7-V-2006
10	Forest trail to Torregarcía, eastern area	30SWF632758	8-III-1997
11	Rambla de Amoladeras, right bank	30SWF638754	5-X-2001, 19-VI-2002, 2-IX-2002
12	Playa de Amoladeras	30SWF643748	22-IV-2002
13	Bunker of Amoladeras	30SWF65174	13-IV-1994, 22-IV-2002
14	Ornithological Refuge of Amoladeras and Viewpoint	30SWF654762	21-IV-2000, 4-IX-2003, 6-XI-2004
15	Amoladeras, Beacon	30SWF655768	4-IX-2003
16	Amoladeras, 1 km upstream from Ornithological Refuge	30SWF656776	4-IX-2003
17	Playa de El Charco	30SWF660732	22-IV-2002
18	Amoladeras Interpretation Center	30SWF666753	19-IX-1996
19	Right bank of El Charco lagoon	30SWF664730	22-IV-2002, 1-V-2002
20	Left bank of El Charco lagoon	30SWF670730	10-IV-2002, 6-VI-2002, 1-VIII-2002
21	Mazarulleque	30SWF667742	12-I-2002, 7-XII-2003
22	Cabo de Gata village, NW	30SWF673714	16-IX-1995, 3-III-1996
23	Cabo de Gata village, NE	30SWF680715	7-VIII-2006
24	Rambla Morales upstream from Torre Marcelo	30SWF675742	23-III-2002
25	Torre Marcelo	30SWF686743	11-III-1997, 20-VI-2002
26	Pujaire	30SWF688718	20-V-2000
27	Playa de Las Salinas	30SWF689696	12-X-1996
28	Ornithological Observatory, Las Salinas	30SWF695685	31-VIII-1997
29	El Barranquete village	30SWF655768	14-XII-1997
30	Rambla del Hacho, El Barranquete	30SWF722779	17-IV-1994

Collections. Studied material has been deposited in the Museo Nacional de Ciencias Naturales (MNCN) collection and D. Moreno collection.

RESULTS

The population of *T. subdentata helicella* living in El Alquián, Almería (Spain), was found in March 1994. Subsequent exploration of the area showed that this taxon was distributed over a wider area than previously reported, including the Cabo de Gata-Níjar Natural Park (Figs. 1-6).

Shell characters

In all localities in which the species is found (Table II), the shell of *T. s. helicella* (Figs. 2, 3, 7–30) is depressed, with 4-5 whorls, and a sharp keel at the periphery. The aperture is elliptical with a slight angle corresponding to the

Tabla I. Localidades de muestreo en el área de estudio, de oeste a este, con coordenadas UTM, fecha de recolección, una breve descripción del sustrato y las especies vegetales dominantes. Todas las localidades pertenecen a la provincia de Almería. Las localidades 7, 8, 10-23 y 25-28 se encuentran dentro del Parque Natural de Cabo de Gata-Níjar.

Nº	Substratum	Vegetation
1	Sand and dunes	*Thymelaea hirsuta, Launaea* sp., *Ammophila arenaria*
2	Sand and dunes	*Thymelaea hirsuta, Ammophila arenaria*
3	Sand and dunes	*Thymelaea hirsuta, Tamarix* sp.
4	Sand and dunes	*Thymelaea hirsuta,* Launaea sp.
5	Sand and dunes	*Agave* sp., *Nicotiana glauca, Thymelaea hirsuta*
6	Uncultivated land	*Thymelaea hirsuta, Launaea* sp.
7	Sand and dunes	*Thymelaea hirsuta, Ononis natrix*
8	Sand and dunes	*Thymelaea hirsuta, Ziziphus lotus*
9	Rocky rambla	*Launaea* sp., *Nerium oleander, Stipa tenacissima*
10	Sand and dunes	*Thymelaea hirsuta, Ziziphus lotus*
11	Rocky rambla and sand	*Thymelaea hirsuta, Ammophila* arenaria, *Juncus* sp.
12	Sand and dunes	*Ononis natrix, Thymelaea hirsuta*
13	Sand and dunes	*Ononis natrix, Thymelaea hirsuta*
14	Uncultivated land	*Thymelaea hirsuta, Launaea* sp., *Stipa tenacissima*
15	Uncultivated land	*Thymelaea hirsuta, Launaea* sp., *Stipa tenacissima*
16	Rambla	*Nerium oleander, Launaea* sp.
17	Sand and dunes	*Ononis natrix, Thymelaea hirsuta*
18	Sand and dunes	*Thymelaea hirsuta, Launaea* sp., *Agave* sp.
19	Sand and dunes	*Imperata cylindrica, Limonium* sp. and *Salsola* sp.
20	Sand and dunes	*Ononis natrix, Thymelaea hirsuta*
21	Sand and dunes	*Androcymbium europaeum, Ziziphus lotus*
22	Sand and dunes	*Phoenix dactylifera, Ononis natrix*
23	Sand and dunes	*Tamarix* sp., *Juncus* sp.
24	Rambla	*Tamarix* sp., *Salsola* sp.
25	Uncultivated land	*Foeniculum vulgare*
26	Uncultivated land	*Thymelaea hirsuta, Launaea* sp., *Eucalyptus* sp.
27	Sand and dunes	*Ononis natrix, Thymelaea hirsuta*
28	Sand and dunes	*Ononis natrix, Thymelaea hirsuta*
29	Uncultivated land	*Androcymbium europaeum, Thymelaea hirsuta, Launaea* sp.
30	Rocky conglomerates	*Thymelaea hirsuta, Launaea* sp., *Stipa tenacissima*

carina. The lip is thickened inside. Sometimes the last half of the body whorl clearly grows below the carina of the anterior whorl (see also Fig. 37). Shell surface is glossy and has a very light reticulate sculpture, which is only visible with a magnifying glass, stereomicroscope or SEM. The sculpture is formed by regular spiral streaks and broader, but more irregular, radial ribs (Fig. 37-38). The umbilicus is always closed. The maximum diameter of the shell ranges from 17 to 21 mm in adult specimens.

The colour of the spire, the keel and the outer lip is usually white in apical view, while at least the last half of the body whorl below the carina is pale brown to dark orange. Sometimes (less than 5% of shells), the spire has a light brown to orange spiral band (the central part is occasionally dark) near the carina. When this band is present, there are usually 2-6 dark spiral bands at the

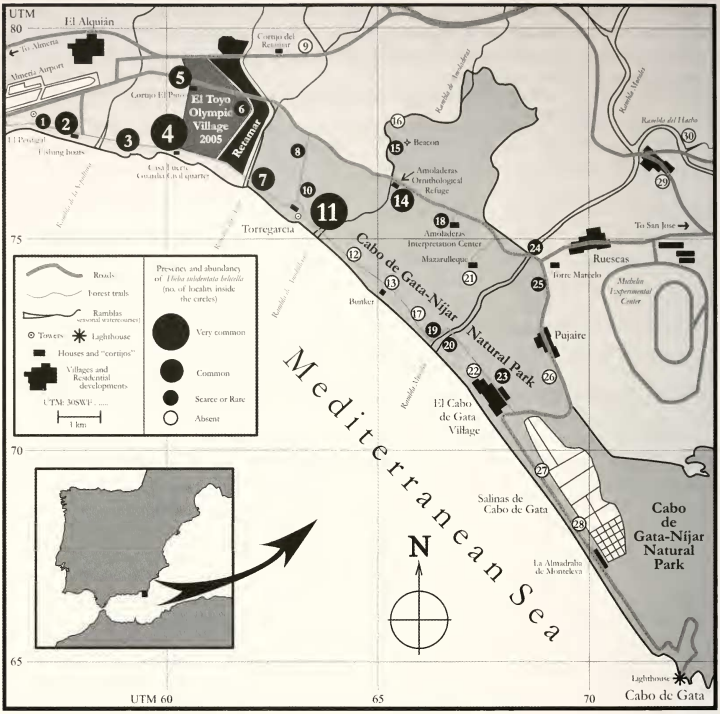


Figure 1. Map showing the study localities in the Eastern area of Almería Bay including the Western part of the Cabo de Gata-Níjar Natural Park, and estimated abundance of *Theba subdentata helicella*: rare or scarce (1-10 specimens), common (11-100 specimens), very common (more than 100 specimens) (see Tables I or II for locality numbers).

Figura 1. Mapa mostrando las localidades estudiadas en el área oriental de la bahía de Almería, incluyendo la parte occidental del Parque Natural de Cabo de Gata-Níjar, y estima de abundancia de Theba subdentata helicella*: rara o escasa (1-10 ejemplares), común (11-100 ejemplares), muy común (más de 100 ejemplares) (ver Tablas I o II para los números de localidad).*

base below the carina. The interior of the aperture is pink.

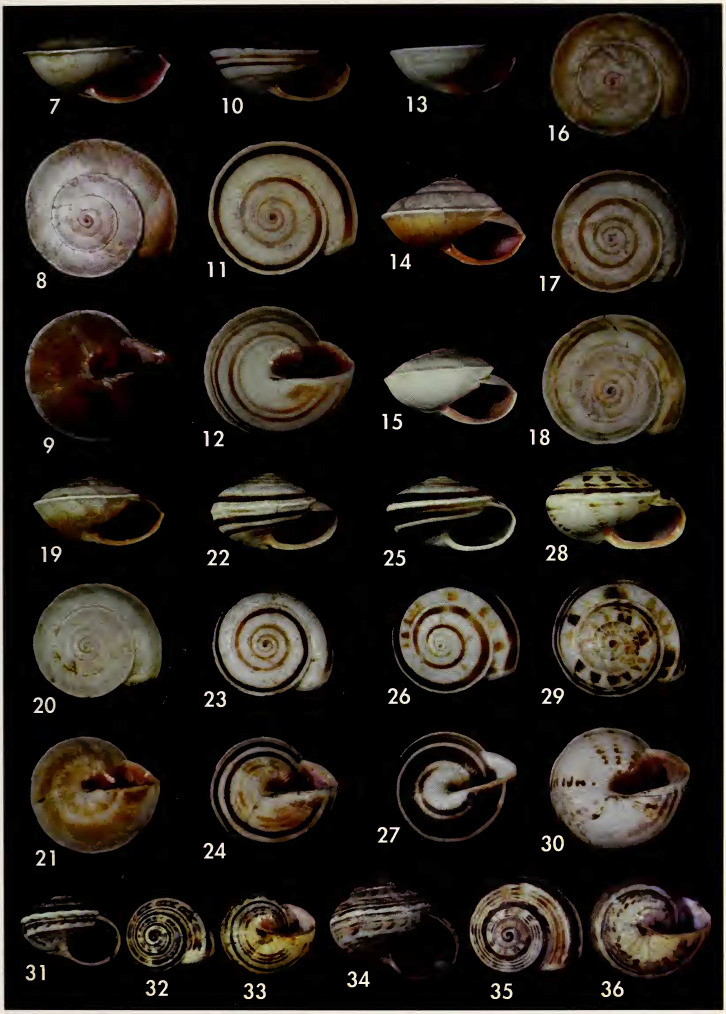
The protoconch is clearly distinguished from the teleoconch by both colour and microsculture. The protoconch is purple to pinkish in live specimens or fresh shells. It has 1.7 whorls and is almost smooth (Fig. 39). Only very light radial ribs can be observed close to the suture with the protoconch nucleus (Fig. 40). Total width is around 1.6 mm and the width of nucleus is approximately 300 microns. The transition to the teleoconch is frequently very abrupt.

We only observed variation in shell shape in the population from the Rambla de Amoladeras (localities 11 and 14), with a gradation from the usual depressed, sharply keeled specimens (see above) to taller specimens with a

Table II. Presence of *Theba subdentata helicella* and other land snails in the study area. Codes of estimated abundance: X (rare, 1-2 specimens), XX (scarce, 3-10 specimens), XXX (common, 11-100 specimens), XXXX (very common, more than 100 specimens).
Tabla II. Presencia de Theba subdentata helicella *y otros gasterópodos terrestres en el área de estudio. Códigos estimados de abundancia: X (raro, 1-2 ejemplares), XX (escaso, 3-10 ejemplares), XXX (común, 11-100 ejemplares), XXXX (muy común, más de 100 ejemplares).*

Nº	Localities	*Sphincterochila candidissima*	*Sphincterochila boetica*	*Caracollina lenticula*	*Cochlicella acuta*	*Cochlicella conoidea*	*Microxeromagna armillata*	*Helicella madritensis*	*Helicella stiparum*	*Xerosecta adolfi*	*Cernuella virgata*	*Otala lactea murcica*	*Theba pisana pisana*	*Theba* sp.	*Theba subdentata helicella*	*Iberus gualterianus* ecotype *alonensis*	*Rumina decollata*	*Ferussacia folliculo*	Number of species
1	Torre del Perdigal, El Alquián				xxx		xx		xx			xx		xxx	xx		x		7
2	Playa de El Alquián, fishing boats area													xxx	xxx				2
3	Dunes between El Alquián-Casa Fuerte													xx	xxx				2
4	Casa Fuerte, El Alquián	x												xx	xxxx				3
5	Cortijo el Pino, El Toyo													xxx	xxx				2
6	Urbanización de Retamar	xxx						xx	xx			xxx			xx				5
7	Rambla del Agua, Retamar						x		xxx					xxx	xxx				4
8	Forest trail to Torregarcía, western area				xx				xxx			xxx		xxx	xx				5
9	Cortijo del Retamar	xxx		xxx	xx		xx	xx	xxx			xx	xx				xx	x	10
10	Forest trail to Torregarcía, eastern area														xx				1
11	Rambla de Amoladeras, right bank				x				x			x		xxx	xxx				5
12	Playa de Amoladeras													xxx					1
13	Bunker of Amoladeras													xxx					1
14	Ornithological Refuge of Amoladeras and Viewpoint	x	x	x	xx		x		xx			x		xx	xxx		x		10
15	Amoladeras, Beacon	x						x	xx			x	x		x				6
16	Amoladeras, 1 km upstream from Ornithological Refuge											x							1
17	Playa de El Charco													xx					1
18	Amoladeras Interpretation Center													xxx	x				2
19	Right bank of El Charco lagoon				xxx		xx							xxx	xx				4
20	Left bank of El Charco lagoon			x	xxx					xxx	xxx	x		xxx	x				7
21	Mazarulleque				xxx				xx					xxxx					3
22	Cabo de Gata village, NW			x	xx	xx								xxxx					4
23	Cabo de Gata village, NE													xxx	xxx				2
24	Rambla Morales upstream from Torre Marcelo		x		x				x		xxx	xx	xx		xx				7
25	Torre Marcelo				xx							xx	xxxx		xxx				4
26	Pujaire				x					xx		xxx	xxx				xxx		5
27	Playa de Las Salinas					xxx						x		xxxx					3
28	Ornithological Observatory, Las Salinas											xxx		xxx					2
29	El Barranquete village	xx			xx							xxx	xxx						4
30	Rambla del Hacho, El Barranquete											x				xx			2
	Number of localities:	6	2	4	13	2	5	3	10	2	2	16	6	20	18	1	4	1	

Figures 2-6. *Theba subdentata helicella*. 2, 3: living animals from Casa Fuerte, El Alquián, Almería; 4, 5: typical habitat and maximum abundance on bushes of *Thymelaea hirsuta*; 6: syntopic population of *Theba subdentata helicella* and *Theba* sp. on *Foeniculum vulgare*, at Rambla de Amoladeras, Almería. *Figuras 2-6.* Theba subdentata helicella. *2, 3: animales vivos en Casa Fuerte, El Alquián, Almería; 4, 5: hábitat típico y máxima abundancia sobre el arbusto* Thymelaea hirsuta*; 6:* Theba subdentata helicella *and* Theba *sp., juntos sobre* Foeniculum vulgare, *en la Rambla de Amoladeras, Almería.*



Figures 7-36. Shells of *Theba* spp. from El Alquián and Cabo de Gata, Almería. 7-18: *Theba subdentata helicella* from Casa Fuerte, El Alquián; 19-30: *T. s. helicella* from right bank of Rambla de Amoladeras; 31-33: *Theba* sp. from right bank of Rambla de Amoladeras; 34-36: *Theba pisana pisana* from Torre Marcelo.

Figuras 7-36. Conchas de Theba *spp. from El Alquián y Cabo de Gata, Almería. 7-18:* Theba subdentata helicella *de Casa Fuerte, El Alquián; 19-30:* T. s. helicella *de la Rambla de Amoladeras; 31-33:* Theba *sp. de la Rambla de Amoladeras; 34-36:* Theba pisana pisana *de Torre Marcelo.*

very slight keel, nearly absent, only visible on the last half of the body whorl near the aperture. The colour of these specimens is also variable, from white specimens (with orange base) to specimens with two dark spiral bands above the keel, dark spirally arranged blotches near the suture and 3-8 dark spiral bands at the base. The basal bands can be simple (Fig. 24, 27) or, more rarely, composed of blotches, or united forming only two broad spiral bands (Fig. 30).

Soft parts characters

The animal of *T. s. helicella* is long and narrow (Figs. 2-3), light grey, darker on the mantle and on the area of the head between the tentacles. All four tentacles have a retractor muscle that is pigmented in a dark grey colour, almost black, more evident in the upper pair than can be observed through the transparent body wall. There are no differences in body pigmentation between individuals having different colour patterns in the shells (dorsal part white or with bands).

Genital system characters

Five specimens from Rambla Amoladeras were dissected and the different organs of the genital system were measured (Fig. 45-52, Table IV). The penis is more or less spindle shaped; proximally it is enlarged to different degrees (Figs. 45-46), while distally it becomes distinctly slender, as thin as the epiphallus. The inside of the penis shows strong radial pleats (Fig. 47, 52) and a penial papilla at its thinner distal part. The penis retractor muscle at the insertion point of the penis thickens slightly. The length of the penis retractor muscle varies greatly (from eight mm to more than twice this length). The flagellum is thin and longer than the penis and epiphallus combined (frequently over twice as long). The flagellum is somewhat longer than the relatively thick and long pair of mucous glands. The distal end was bifid in one specimen (Fig. 48). The proximal part of the bursa copulatrix duct has an enlarged base and is clearly shorter than its relatively thin distal part. The diverticulum is wide and enlarges distally; it is longer than the distal part of the duct and thus reaches beyond the bursa copulatrix, which is rounded to a pyriform shape. The free oviduct is thin and visibly shorter than the vagina, which is two-thirds to almost twice its length. The dart sac is relatively small, 3 mm in length on average. The uterus and prostate form a characteristic loop close to the albumen gland, which is long, slender, and tongue-shaped. The vesicula seminalis is very darkly pigmented and measures from 1.4 to 1.9 mm. The hermaphrodite duct ends near its distal part (Figs. 45, 50 - 51).

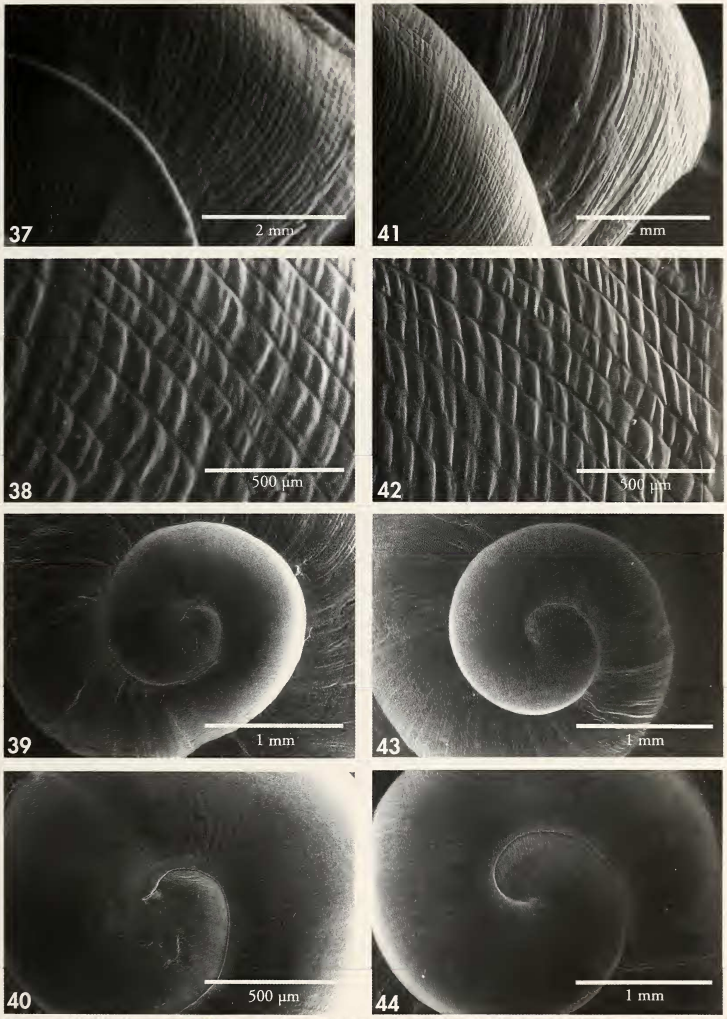
In its resting position (as the genital system is situated inside the animal) (Fig. 49), the proximal part of the flagellum makes a characteristic loop around the penis retractor muscle. The fold made by the diverticulum around the proximal part of the uterus is also quite characteristic. Figure 50 shows this fold as well as the diameter differences between the proximal part of the bursa copulatrix duct and the diverticulum.

Habitat and ecology

Theba s. helicella lives in a narrow strip of land, about 2-3 km wide, near the sea. The coastal area is characterized by sand beaches, dunes and "ramblas" (seasonal watercourses) where the vegetation has African elements (as *Ziziphus lotus*). The climate is semiarid with very scanty rainfall.

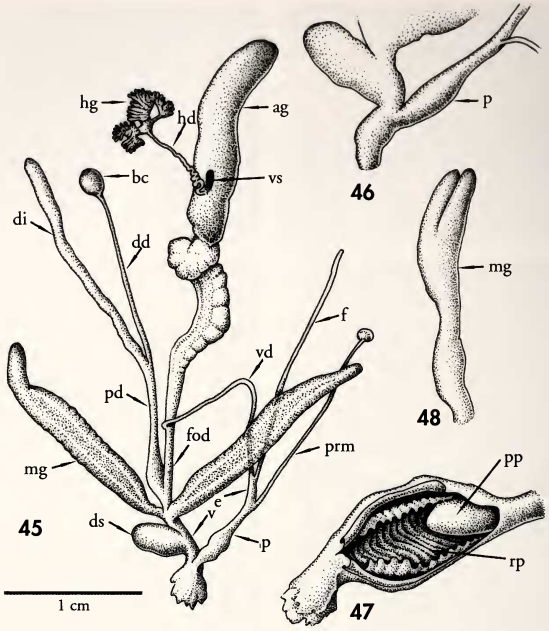
This species is very common on *Thymelaea hirsuta*, *Ziziphus lotus*, *Launaea* sp. and other bushes. It is also observed on grasses, as *Ammophila arenaria*, *Imperata cylindrica* and *Stipa tenacissima*, rushes, as *Juncus* sp., small trees, as *Tamarix* sp. and *Nicotiana glauca* (invasive species) or on introduced species as *Agave* sp.

In Rambla de Amoladeras, *T. s. helicella* is common, with shells and live specimens on sand and *Ammophila arenaria*, *Juncus* sp., *Thymelaea hirsuta*, *Ziziphus lotus* and other bushes. There are some specimens of *T. s. helicella* without keel that are only found near rock outcrops which are originated by tectonic



Figures 37-44. Scanning Electron photomicrographs of the shell microsculpture of body and penultimate whorls, detail of reticular microsculture, protoconch and protoconch microsculpture. 37-40: *Theba subdentata helicella* from right bank of Rambla de Amoladeras; 41-44: *Theba pisana pisana* from Torre Marcelo.

Figuras 37-44. Fotomicrografías con microscopio electrónico de barrido de la microescultura de la concha y penúltima vuelta, detalle de la microescultura reticular, protoconcha y microescultura de la protoconcha. 37-40: Theba subdentata helicella *de Rambla de Amoladeras; 41-44:* Theba pisana pisana *de Torre Marcelo.*



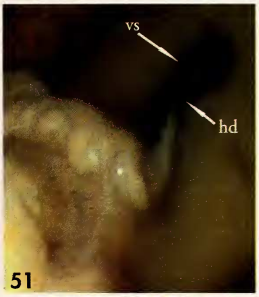
Figures 45-48. Genital anatomy of *Theba subdentata helicella* from right bank of Rambla de Amoladeras (see Abbreviations in Material and methods).
Figuras 45-48. Anatomía del sistema genital de Theba subdentata helicella *de Rambla de Amoladeras (ver abreviaturas en Material y métodos).*

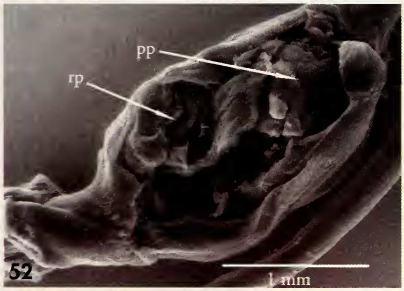
faults in the bedrock, or by Pleistocene conglomerates of ancient beaches. The most variable population lives in this locality.

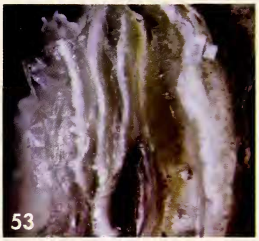
Snails are active mainly in autumn (October) when the rainfall is more frequent and abundant in the area. Usually in autumn, the individuals are withdrawn inside the shell on the sand between bushes during the day and are active during the night. In spring and summer, all live specimens, including juveniles, are adhered to trunks of bushes, at the shady base or on the illuminated branches, reaching more than one meter above the ground, generally with the apex towards the ground. The adherence is so strong that it is often impossible to remove them without breaking the shell or plucking out the cortex (patch to the epiphragm). The definitive epiphragm is thick, composed of several layers (up to 5-6) of dried, transperant, film mucus, each of which have a thin, external white calcareous layer (Fig. 53). This type of epiphragm, adapted to extreme climates, is more complex than that of other *Theba* species.

Distribution and conservation status

In the study area, *T. s. helicella* lives in the coastal zone between Torre del







Figures 49-53. Genital system and epiphragma of *Theba subdentata helicella* from right bank of Rambla de Amoladeras. 49: stereomicroscope images of the complete genital system; 50: detail of the hermaphrodite gonad and sperm-oviduct in relation to the vesicula seminalis, showing the natural position of the folds of the diverticulum (di) and the distal part of the bursa copulatrix duct (dd); 51: detail of the vesicula seminalis (vs) and distal part of hermaphrodite duct (hd); 52: scanning electron micrograph of the inner part of the penis, showing the radial pleats (rp) and the penis papilla (pp); 53: epiphragm with several layers to avoid dessication.

Figuras 49-53. Sistema genital y epifragma de Theba subdentata helicella *de Rambla de Amoladeras. 49: Imagen de estereomicroscopio del sistema genital completo. 50: detalle de la gónada hermafrodita y del espermiducto en relación a la vesícula seminal, mostrando la posición natural del diverticulo (di) y de la parte distal del conducto de la bursa copulatrix (dd); 51: detalle de la vesícula seminal (vs) y parte distal del conducto hermafrodita (hd); 52: fotomicrografías con microscopio electrónico de barrido de la parte interna del pene, mostrando los pliegues radiales (rp) y la papila penial (pp); 53: epifragma con varias capas para evitar la desecación.*

Perdigal and Rambla Morales, corresponding to an area of 12 km long, and between 1 km width at the west (El Alquián, where the Almería airport limits its northerly distribution) to 3 km width at the east (Rambla Morales) (Fig. 1).

In the east part of Almería Bay, the center of distribution of the species is Casa Fuerte. This locality sheltered the population with a very high density of specimens, but the El Toyo Olympic Village was built over it in 2005. However, our investigations confirm the presence in several localities inside the Cabo de Gata-Níjar Natural Park, between Amoladeras and Morales watercourses. This protected area, one of the more important natural parks of Andalusia, was declared in 1987. We suggest here to include this subspecies in the National and in the Andalusian Lists of Threatened Species, and in the Conservation Plan (Plan de Ordenación de los Recursos Naturales, PORN) for the Cabo de Gata-Níjar Natural Park. The International Union for Conservation of Nature (IUCN) criteria proposed here for this taxon is: Vulnerable A2ac; B2ab(ii,iii,iv). Also, it is important to periodically monitor all the populations and to reinforce vigilance in the conservation of this taxon. The park inhabitants often collect snails for food (*T. p. pisana*, *Otala lactea murcica* and *Iberus gualtieranus* ecotype *alonensis*) after the few rainy days during the year, although this is forbidden.

Other molluscs species in the study area

A total of 17 species of land snails, included *T. s. helicella*, have been found in the study area (Table II).

Sphincterochila (Albea) candidissima (Draparnaud, 1801). This is a widely distributed species in the Mediterranean Basin, that is also very common in the SE area of Andalusia (Ruiz, Cárcaba, Porras and Arrébola, 2006) and in the Almería province (Montero, Oña, Pina, Román and Segura, 1986). We have found it in El Alquián, Retamar area, Ornithological Refuge of Amoladeras, in the Amoladeras beacon and in Barranquete. It seems to be more abundant inland in less sandy zones.

Sphincterochila (Cariosula) baetica (Rossmässler,1854). This species lives in the SE of Spain and in North Africa (Morocco and NW of Algeria). In Andalusia it lives only in the south part of the Almería province (Ruiz *et al.*, 2006). This species is quite similar to *S. candidissima*. The shell of *S. baetica* has thin and irregular brown blotches on the dorsal surface, and a brownish protoconch, while *S. candidissima* has a smooth shell and protoconch and is uniformly white. In the study area, it has been found in the Ornithological Refuge of Amoladeras and on the rocky shores of Rambla Morales. Active specimens were observed in the rainy period of October in Rambla Morales.

Caracollina (Caracollina) lenticula (Michaud, 1831). This is a widely distributed species in the Mediterranean Basin, that is present throughout Andalusia (Ruiz *et al.*, 2006). *C. lenticula* is a small, lentil-shaped land snail, very rare in sandy zones as the left bank of El Charco lagoon of the Rambla Morales and the surrounding areas of Cabo de Gata village, and more abundant in rocky areas or ramblas as the Ornithological Refuge of Amoladeras and Cortijo del Retamar.

Cochlicella (Cochlicella) acuta (O.F. Müller, 1774). This species, widely distributed in Europe, lives in all the lower areas of Andalusia (Ruiz *et al.*, 2006). *Cochlicella acuta* is abundant in the study area, mainly in sandy zones near the beach (El Perdigal), and the shores of the Rambla de Amoladeras and Rambla Morales, although it has also been found in more anthropic areas such as uncultivated lands (Pujaire), gutters (Torre Marcelo) and more inland zones (El Barranquete).

Cochlicella (Cochlicella) conoidea (Draparnaud, 1801). This species is widely

distributed in the Western Mediterranean and in the Atlantic Portuguese areas. In Andalusia it lives in almost all the littoral (RUIZ *ET AL.*, 2006). We have found specimens, taller than the typical shape, in sandy zones close to Playa de Las Salinas and Cabo de Gata village.

Microxeromagna armillata (Lowe, 1852). This species, widely distributed in the Western Mediterranean, is present in all Andalusia region (RUIZ *ET AL.*, 2006). *Microxeromagna armillata* has been found in five localities: in Torre del Perdigal (El Alquián) and in four localities of Cabo de Gata-Níjar Natural Park (Table II). It lives in sandy biotopes near the littoral zone.

Helicella madritensis (Rambur, 1868). This species is widely distributed in the Iberian Peninsula and was recorded in the central (Alhama) and Northern parts of Almería (María and Vélez) (PUENTE, 1994). Its distribution in Andalusia is restricted to Eastern areas (mainly Almería province), included the Cabo de Gata-Níjar Natural Park (RUIZ *ET AL.*, 2006). It has been found in the Retamar area in two localities and the Amoladeras beacon.

Helicella stiparum (Rossmässler, 1854). This species is endemic to Almería, and has been recorded in a few localities in the Almería Bay, in its occidental area (APARICIO AND RAMOS, 1987; PUENTE, 1994; ARRÉBOLA, 2002) and oriental part (RUIZ *ET AL.*, 2006). The species is frequent in the study area where it has been found in ten different localities, both in sandy and rocky areas. The shell is usually uniformly white though specimens found close to the Amoladeras beacon and Retamar area exhibit brown irregular bands above the keel. Active specimens were found in October, the rainy period, in Rambla Morales.

Xerosecta (Xeromagna) adolfi (Pfeiffer, 1854). This species is endemic to Almería, and has only been recorded in a few localities of the central and Western part of Almería Bay (PUENTE, 1995; RUIZ *ET AL.*, 2006). In the study area, it is relatively abundant on the left bank of Rambla Morales and in uncultivated lands at Pujaire. This is the first record of the species in the Cabo de Gata-Níjar Natural Park.

Cernuella (Cernuella) virgata (Da Costa, 1778). This species is widely distributed in Europe and North Africa, and is present throughout Andalusia region (RUIZ *ET AL.*, 2006). It is relatively abundant along the left bank of Rambla Morales up to Torre Marcelo.

Otala (Otala) lactea murcica (Rossmässler, 1854). This widely distributed species has two subspecies in Andalusia region: *O. l. lactea* (O.F. Muller, 1774) and *O. l. murcica*. The last subspecies is characterized by a larger shell with a spread outer lip, and lives only in the Eastern area of Andalusia, in the Almería province (RUIZ *ET AL.*, 2006). This gastropod was found in many localities of the study area although it is scarce in sandy areas and more frequent in rocky areas at higher altitudes and in the "ramblas" shores. It has been observed alive and spawning in October at Rambla Morales.

Theba pisana pisana (O.F. Müller, 1774). This subspecies has a wide distribution in the Mediterranean Basin, and lives throughout Andalusia region (RUIZ *ET AL.*, 2006). The shell is globular with a very variable pigmentation from clear to banded and spotted specimens (Figs. 34-36). In the study area it is very common, always far from the sea, in uncultivated lands, close to farms and in gutters along the roads, as in Torre Marcelo, where it lives with *T. s. helicella*.

Theba sp. In the study area there is another *Theba* species, that lives in littoral areas in sand substrates. This taxon is characterized by a small and globular shell, with a flattened spire and an incipient keel (Figs. 31-33). The umbilicus is circular and open. PUENTE (1994) considered it to be a new species, but it

Table III. Descriptive statistical data of shell measurements (Appendix I) for the studied populations of *Theba subdentata helicella* (Casa Fuerte) (THC), *T. s. helicella* (Rambla Amoladeras) (THA) and *Theba pisana pisana* (Torre Marcelo) (TPM).
Tabla III. Datos estadísticos descriptivos de las medidas de la concha (Apéndice I) de las poblaciones estudiadas de Theba subdentata helicella *(Casa Fuerte) (THC),* T. s. helicella *(Rambla Amoladeras) (THA) y* Theba pisana pisana *(Torre Marcelo) (TPM).*

	Theba subdentata helicella (Casa Fuerte) (n = 30)			*Theba subdentata helicella* (Rambla Amoladeras) (n = 30)			*Theba pisana pisana* (Torre Marcelo) (n = 30)		
	Mean±SD	Range	Coeff. Variation	Mean±SD	Range	Coeff. Variation	Mean±SD	Range	Coeff. Variation
NSW	4.85±0.16	4.50-5.15	0.030	4.83±0.21	4.5-5.15	0.040	4.89±0.27	4.30-5.45	0.060
SW (mm)	19.06±0.91	16.75-20.82	0.048	17.98±0.92	16.54-19.75	0.054	16.1±1.2	13.83-18.75	0.074
SH (mm)	10.22±0.55	8.83-11.42	0.054	10.64±0.54	9.59-11.95	0.050	12.1±1.26	10.27-1.49	0.104
UD (mm)	0	–	–	0	–	–	1.1±0.2	0.80-1.60	0.200
WBW (mm)	12.27±0.67	10.90-13.47	0.054	12.17±0.7	10.8-13.93	0.058	10.67±0.78	8.85-12.14	0.070
AW (mm)	9.6±0.5	8.4-10.7	0.100	9.0±0.6	8.3-10.3	0.100	8.1±0.6	7.3-9.4	0.100
AH (mm)	6.5±0.4	5.6-7.2	0.100	5.3±0.5	4.3-6.2	0.100	7.5±0.7	6.0-9.0	0.100

has not been described yet. The name *Theba pisana ampullacea* (Pallary, 1915) was used by Gittenberger and Ripken (1987) and Gittemberger, Ripken and Bueno (1992) for a subspecies characterized by a smaller shell, that inhabits the Western coast of Morocco, from Essauira to near Tiznit, sympatric with *T. s. subdentata*, *T. s. helicella* and *T. s. dehnei*. So, therefore, the taxon present in Almería coast could be a subspecies of *T. pisana* or a new species. In the study area, this taxon lives in several localities together with *T. s. helicella*, frequently on the same shrub (Fig. 6). This small taxon, very abundant in some localities, is rarely observed alive during the summer because they live buried or under bush branches during this period.

Iberus gualtieranus (Linnaeus, 1758) ecotype *alonensis* (Férussac, 1821). This ecotype has a wide distribution along the Mediterranean coast of Spain and is the dominant taxa in the mountains close to Níjar (Rambla del Hacho and El Barranquete in this paper), as well as in the mountains of Cabo de Gata (Cobos, 1979; Montero *et al.*, 1986). It has not been found in sandy zones of Almería Bay.

Rumina decollata (Linnaeus, 1758). This species lives throughout the Mediterranean Basin, and throughout Andalusia region (Ruiz *et al.*, 2006). In the study area, it has been found in scattered locatities from Perdigal (sandy zone close to the beach), Ornithological Refuge of Amoladeras (rocky zone) and Pujaire (abandoned farms) where it is most abundant.

Ferussacia (Ferussacia) follicula (Gmelin, 1791). This is a widely distributed species in the Mediterranean Basin, living throughout Andalusia region (Ruiz *et al.*, 2006). In the study area a few specimens were observed in a wet "rambla" next to de Cortijo del Retamar.

Among all the taxa present in the study area the most abundant seems to be *Theba* sp. It was present in 20 out of the 30 localities (Table II). Next to this, the taxon with the widest distribution in the Eastern part of the Almería Bay is *T. s. helicella* (present in 18 localities), followed by *O. l. murcica* (16), *C. acuta* (13) and *H. stiparum* (10). *Iberus g.* ecotype *alonensis* and *F. follicula* were only present in one locality.

Only two localities (both "ramblas") hold 10 different taxa: Ornithological Refuge of Amoladeras and Cortijo del Retamar (Table II). Next to this, three localities have seven different taxa: Torre del Perdigal, the left bank of El Charco lagoon, and Rambla Morales upstream from Torre Marcelo. All these areas are more or less far from the sea. The localities next to the sea, with a very dry habitat and sandy susbstratum, have only 1-3 taxa of land snails.

DISCUSSION

Taxonomical characters

Shell characters of *T. s. helicella* are rather constant in all of the studied populations except in Rambla de Amoladeras (localities 11 and 14). Here, in rocky areas, there is a gradation in shell shape and colour from the whitish, depressed, sharply keeled specimens with an orange base, to taller specimens with a pattern of spiral brown bands and a nearly absent keel, only visible on the last half of the body whorl near the aperture. This gradual variation is similar to that described by GITTENBERGER AND RIPKEN (1987) for Moroccan populations of *T. s. helicella* (with a sharp keel) and *T. s. dehnei* (with flattened to moderately convex whorls, an inflated body whorl whose periphery is angular to regularly rounded at the beginning; aperture broad elliptical), with intermediate forms near Essaouira (= Mogador). These authors published photographs (their figs. 22-24) showing the range of variation found in a fossil population from Safi (Morocco). According to these authors, *T. s. helicella*, with a sharply keeled shell, is represented in sand dunes along the coast while *T. s. dehnei* lives in more rocky habitats. In places where sand dunes and rocky areas come together, there are intermediate forms between *T. s. helicella* and *T. s. dehnei*. Along the Rambla de Amoladeras the substratum varies gradually from sand dunes at the ancient pit to a rocky substratum at the Ornithological Refuge, where Pleistocene conglomerates are mixed with sand dunes. This is the only locality in the study area having rocky areas near the coast. It may be possible that the presence of the inflated specimens with a very slight keel in the last half whorl and a blotch-like colour pattern, is associated with the rocky substratum of Rambla de Amoladeras banks. These are the only specimens studied that are similar in shell colour and shape to the subspecies *T. s. dehnei.*

The adaptation to rocky substratum described here is similar, but the opposite to the gradual variation reported for *Iberus gualtieranus* (Linnaeus, 1758) in the mountains of Sierra de Gador (Almería), Sierra Elvira (Granada) and Sierra de Jaén (Jaén) where sharply keeled specimens (ecotype *gualtieranus*) are found at the rocky, karstic and hot areas whereas rounded, inflated specimens (ecotype *alonensis*) are the usual forms in cooler and non-karstic areas, with intermediate shells at intermediate habitat (LÓPEZ-ALCÁNTARA, RIVAS, ALONSO AND IBÁÑEZ, 1985). The presence of a keel in this species was described as an adaptation to rocky fissures for protection against drought in the insolated and karstic areas, with scarce vegetation. There is, however, a similarity to the shell variation of *I. gualtieranus* as the keeled specimens of this species have no bands (as occurs with the typical form of *T. s. helicella*) while the rounded specimens have a pattern of spiral brown bands. In the polymorphic species *Cepaea nemoralis* (Linnaeus, 1758) the yellow or light pink specimens with or without unfused bands are found in the more insolated habitats whereas the darker coloured specimens with dark bands, frequently heavily fused, are associated with more protected shaded forest habitats in Spain. This variation has been related to a physiological adaptation to the biotopes (RAMOS, 1984, 1985) related to absorption of energy from the sunrays. If this is the case in *T. s helicella*, then the absence of bands could be advantageous in the heavily sunny sandy areas, where the specimens form dense aggregations on herbaceous plants, whereas

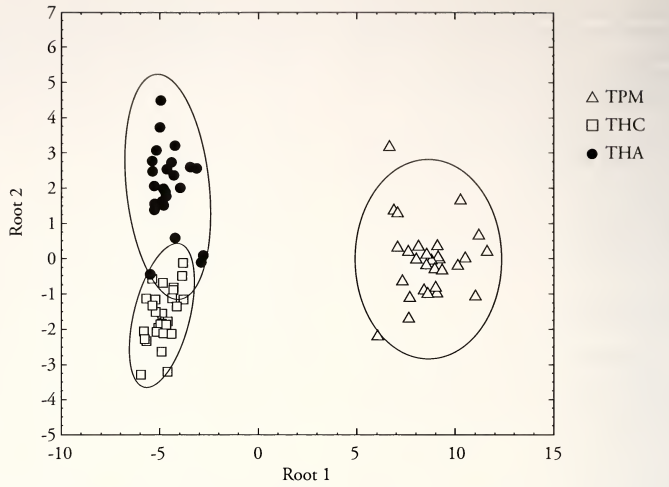


Figure 54. Plot of discriminant scores on the two canonical axes, obtained from DFA of shell measurements for the populations of *Theba subdentata helicella* (Casa Fuerte) (THC), *T. s. helicella* (Rambla Amoladeras) (THA) and *Theba pisana pisana* (Torre Marcelo) (TPM). Confidence intervals for ellipses: 0.95.

Figura 54. Representación gráfica en los dos ejes canónicos de los valores obtenidos en el análisis discriminante de las medidas de la concha de las poblaciones de Theba subdentata helicella *(Casa Fuerte) (THC),* T. s. helicella *(Rambla Amoladeras) (THA) y de* Theba pisana pisana *(Torre Marcelo) (TPM). Límites de confianza para las elipses: 0,95.*

the bands might not be a physiological limitation upstream in the Rambla de Amoladeras, where snails can probably find refuge among the rocks and a slightly denser vegetation.

The most rounded specimens in Rambla de Amoladeras have a blotchy colour pattern, similar to some specimens of *T. p. pisana*, and an almost identical shell microsculpture, which might suggest that these specimens are hybrids between the two taxa. However, this hypothesis should be rejected because in the sympatric populations (Table II) the shells, assigned here to *T. s. helicella*, can be clearly distinguished from those of *T. p. pisana* by their larger size, depressed shells, and by the presence of a keel in adult specimens.

To test these hypotheses, conchological differences between the population of *T. s. helicella* from Casa Fuerte (THC), that represents the most common shape of the species in the study area (n = 30), the population from Rambla de Amoladeras watercourse (n = 30) (THA) and the population of *T. pisana* from Torre Marcelo (n = 30) (TPM) were investigated by a discriminant function analysis using the seven standard shell measurements in Appendix 1. Two highly significant discriminant functions (roots) were found (Wilks' lambda = 0.0071, F (14, 146) = 113.38, $p < 0.0000$). For the first function, that accounted for the 95% of explained variance, the characters that contributed (highest weight) were (in order): SW, UD, AH, SH, and AW. For the second function, the order was: SH, AH and much less NSW. The two discriminant functions were highly significant ($p < 0.001$). Of the 87 individuals classified, all of the

Table IV. Measurements of genital characters for the population of Rambla de Amoladeras in Cabo de Gata and for the data on *Theba subdentata helicella* and *Theba subdentata dehnei* from Morocco (Hesse, 1915).
Tabla IV. Medidas de los caracteres del sistema genital de la población de Rambla Amoladeras en Cabo de Gata y de los datos de Theba subdentata helicella *y* Theba subdentata dehnei *de Marruecos (Hesse, 1915).*

Character	*T. s. helicella** Measurements range (mm)	*T. s. dehnei** Measurements range (mm)	Studied population M. range(mm)	Mean±SD (n=5)
Penis	4.5-7	1.5-2	3.84-7	5.48 ± 1.2
Epiphallus	2-3	1.5-3	1-1.21	1.68 ± 0.4
Flagellum	18-22	14-22	16.2-19.13	18.08 ± 1.14
Vas deferens	16-19	nd	10-14	12.17 ± 1.78
Penis retractor muscle	8.3	5.5-7	8.3-16.5	13.16 ± 3.5
Dart sac (Lenght)	3.5-4	4-5	2.3-3.65	3.23 ± 0.53
Dart sac (Width)	2.5	3-3.5	1.1-2.3	1.95 ± 0.19
Mucous glands	9-15	12-16	14.26-18.08	16.52 ± 1.56
Vagina	7.5-9	5.5-7	5-7.3	6.12 ± 0.78
Free oviduct	2-7	3-6	3.5-4.35	3.87 ± 0.39
Proximal duct of bursa copulatrix	7-9	10	7.2-9	8.29 ± 0.66
Distal duct of bursa copulatrix	9.5-16	12-14	11.8-14	12.77 ± 1.01
Bursa copulatrix (Lenght)	1.5-2.5	2	1.6-1.91	1.76 ± 0.12
Bursa copulatrix (Width)	nd	nd	1.2-1.4	1.34 ± 0.08
Diverticulum	14-27	22-31	15.3-17.7	16.31 ± 0.95
Vesicula seminalis	2	2	1.4-1.9	1.61 ± 0.18

nd = no data
* = Data from Hesse (1915) for *Euparypha planata* (Chemnitz, 1795) (= *T. s. helicella*) and *Euparypha dehnei* (Rossmässler, 1846) (= *T. s. dehnei*).

T. pisana and *T. s. helicella* from Casa Fuerte were correctly classified (100%) and 92% of *T. s. helicella* from Amoladeras watercourse were also correctly classified. Two individuals from Rambla de Amoladeras were included in the cluster of THC. On the scatter plot (Fig. 54) three clusters were observed. As expected, *T. p. pisana* is clearly separated from the two populations of *T. s. helicella* mostly by the width of the shells, shape of aperture and the presence of umbilicus, which is absent in the second taxon. The clusters of the two populations of *T. s. helicella* overlap but they show differences in the height of the shell and the height of the aperture. In Casa Fuerte there is little intra-population variation and the shells are flatter than in Rambla de Amoladeras. In this locality the analysis confirmed the variation described above.

Hesse (1915) provided a detailed description of the genital system of both *T. s. helicella* and *T. s. dehnei* including excellent drawings. The descriptions included the range of variation and proportions between measurements of different quantitative anatomical characters. Table IV summarizes these data and the data we have obtained from the population of Amoladeras (locality 11). The genital system of the studied population is very similar to the figure included in Puente, Altonaga, Prieto and Rallo (1994) and shows intermediate quantitative characters between those reported for the two subspecies of Morocco as follows: The penis length of the studied population falls within the range described for *T. s. helicella* and is much longer than in *T. s. dehnei*. The flagellum is more than twice as long as the

penis plus the epiphallus (averaged proportion = 2.62 ± 0.47) as is the case for *T. s. helicella*. The mucous glands are quite long including the range of variation of *T. s. dehnei* and twice the length reported for *T. s. helicella* from Morocco. The flagellum is somewhat longer than the glandulae mucosae as is the case for *T. s. dehnei*. This proportion is quite different in *T. s. helicella* from Morocco in which the flagellum is one and a half to nearly twice as long as the glandulae mucosae. The dart sac of the specimens measured here is smaller than the length and the width previously described for both subspecies. In *T. s. helicella* the proximal plus the distal part of the bursa copulatrix (BC) duct is about two-thirds of the length of the diverticulum, which thus reaches far beyond the BC. In *T. s. dehnei* the full bursa copulatrix duct is only half as long as the diverticulum, which also reaches far beyond the BC. In the specimens from Rambla de Amoladeras the proximal part of the bursa copulatrix duct is similar to *T. s. helicella* and slightly shorter than in *T. s. dehnei;* the range of the distal duct is rather similar to *T. s. dehnei* and falls within the range of *T. s. helicella* from Morocco. The diverticulum of the studied specimens is not as variable in length as it is for the two Moroccan subspecies reaches only slightly beyond the bursa copulatrix.

The comparisons above show that although the studied population shares many anatomical characters with *T. s. dehnei*, the shape of the genital system is more similar to that described by Hesse (1915) for *T. s. helicella*. Considering the conchological characters, all the populations in the study area show the sharply keeled shells characteristic of *T. s. helicella*, except for the specimens in the Rambla Amoladeras where the population is very variable with shells showing a gradation from keeled to globular specimens. This gradual variation from the typical morphology of *T. s. helicella* to shells that are very similar to *T. s. dehnei* might suggest that both morphs belong to a single variable taxon. However, since *T. subdentata* includes another three subspecific taxa in Morocco, *T. s. subdentata* , *T. s. meridionalis* and *T. s. legionaria*, also with intermediate shell characters between them (Gittenberger and Ripken, 1987), we cannot propose the suppression of the subspecific names without proper information for all the taxa found in Morocco. Further studies will also require a molecular analysis to estimate genetic distances between the nominal subspecies and the populations in Cabo de Gata. Therefore, we conclude that, with the available information, the populations in Almería province should be ascribed to *T. s. helicella* (the oldest available name for a subspecies other than the nominotypic one), a variable taxon with the globose ecotype living in more rocky areas

Geographical distribution

Gittenberger and Ripken (1987) concluded that *T. s. helicella* has probably been introduced in Spain. If this is the case, we can also conclude that the species has adapted very well to environmental sub-desertic conditions of the area expanding its range in this province. This hypothesis reinforces our proposal of a single taxon with ecotypes resulting from one unique introduction rather than the result of several introductions, which would have resulted in a higher variability than the one described here.

On the other hand, the south of the Iberian Peninsula shares many taxa from different groups of plants and animals with similar habitats in the North of Africa. The sub-desert areas of Almería are particularly rich in North-African elements. This is the case, for instance, of *Ziziphus lotus*, which is characteristic of the vegetation in the low and sandy habitats of the study area. Some other gastropod species like *C. virgata* or *R. decollata* here reported are also living on both sides of Alboran Sea. Whether this faunistic and floristic similarity is the result of introductions or vicariant events is still a topic of discussion. The conchological and genital variation of the population of *T. s. helicella* described in this paper overlaps with

the available descriptions for *T. s. helicella* and *T. s. dehnei* from Morocco. Therefore, in order to clarify the origin of the populations of *T. s. helicella* in Almería it seems necessary to apply molecular methods to study the genetic and phylogeographical relationships of these populations with the *Theba subdentata* subspecies from Morocco and related taxa.

Even if the presence of *T. s. helicella* in Almería province is due to introduction, it should have been an historic one since the species is well established in this area. This is the only location in Europe and consequently, the species should be considered in the conservation policy plans. It had been included as "Data Deficient" in the recently published National Red List of Endangered Species (VERDÚ AND GALANTE, 2007). It is included in the Andalusian List (ARRÉBOLA AND RUIZ, in press) as "Vulnerable" as it was suggested previously (GÓMEZ *ET AL.*, 2001; ARRÉBOLA, 2002), and in the present paper.

Considerations about the habitat and vegetation

The present study provides new data on the habitat of *T. s. helicella*, present in the sandy littoral with dunes and also in rocky areas and "ramblas", where was observed the highest variability in this land snail. This species lives on several plant species (Table I), including some introduced plants as *Agave* sp. and *Nicotiana glauca*. A vegetal species very common in sandy zones, and in rocky areas also, is *Thymelaea hirsuta* (L.), an evergreen shrub that shields *T. s. helicella* from the high insolation. This shrub species was cited by Menez (2006) in Retamar, Almería. This author cited in El Alquián the shrub *Stauracanthus* sp. (Leguminosae) as the species holding *T. s. helicella*, but no species of this genus lives in Almería province (TALAVERA, AEDO, CASTROVIEJO, ROMERO ZARCO, SÁEZ, SALGUEIRO AND VELAYOS, 1999). Probably the thorny shrub observed and illustrated by MENEZ (2006) is *Launaea* sp. (Compositae).

Considerations on the malacological fauna of Cabo de Gata

Until now, the malacological fauna of the Eastern part of Almería Bay (excluded Cabo de Gata mountains) was poorly characterised. Only a few papers focused on some land snail taxa present in the area. Among them, COBOS (1979) showed the distribution of *Iberus g. alonensis*, MONTERO *ET AL.* (1986), cited *I. g. alonensis* and *S. candidissima*, and GITTENBERGER AND RIPKEN (1987) cited *T. s. helicella* from El Alquián (although the citation was based on shells collected by Altimira and deposited at RMNH; no live specimens were found by these authors). PUENTE *ET AL.* (1998), in the delimitation of biogeographical areas in the Iberian Peninsula on the basis of Helicoidea species, stated Almería (with only nine species plus two endemics not considered) as an isolated subprovince in the wide Extremadura-La Mancha-Andalusia province, due to "the low number of species that it contains, perhaps because of undersampling". In addition to the species cited by PUENTE *ET AL.* (1998) for Almería, and found in the study area (*C. lenticula, C. virgata, M. armillata, I. gualtieranus s.l., O. lactea, T. pisana, H. stiparum* and the endemic *X. adolfi*), the present study cited in the Eastern part of the Almería Bay other species of Helicoidea: *S. candidissima, S. baetica, C. acuta, C. conoidea, H. madritensis, T. s. helicella*, and *T.* sp.

Although there are few papers on the land snails of Almería, and none on its malacological fauna, recently, and after this paper was submitted, RUIZ *ET AL.* (2006) published a book on the land snails of Andalusia, with maps of distribution and new information about the presence of the different taxa in the study area, and cited for the first time several species in the Eastern part of Almería Bay. In any case in the present paper detailed data on these species are provided and *X. adolfi* is record for the first time in the Cabo de Gata-Níjar Natural Park.

In spite of the extreme dryness and scanty rainfall in the study area, the terrestrial malacological fauna of the region is quite rich with species well adapted to the harsh environmental

conditions. Adaptations include finding refuge below stones or brush, burying behaviour, development of thick epiphragms (Fig. 53), slowing of metabolism and reproducing soon after the infrequent rains, particularly in autumn.

The largest population of *T. s. helicella* known in the study area (in Casa Fuerte, El Alquián), has been largely destroyed by the construction of the Olympic Village for the Mediterranean games, held in Almería in 2005. Nevertheless, the populations inhabiting the interior of the Cabo de Gata Natural Park will be preserved by the *ad hoc* legislation, and the survival of the species should be guaranteed.

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Appendix I. Number of shell whorls and shell measurements (in mm) of *Theba subdentata helicella* (Casa Fuerte) (THC), *T. s. helicella* (Rambla de Amoladeras) (THA) and *Theba pisana pisana* (Torre Marcelo) (TPM), AH: aperture height, AW: aperture width (maximum diameter of the aperture), NSW: number of shell whorls, SH: shell height, SW: shell width, UD: Umbilicus diameter, WBW: width of body whorl.

Apéndice I. Número de vueltas de espira y medidas de la concha (en mm) de Theba subdentata helicella *(Casa Fuerte) (THC),* T. s. helicella *(Rambla de Amoladeras) (THA) y* Theba pisana pisana *(Torre Marcelo) (TPM). AH: altura de la abertura, AW: ancho de la abertura (diametro máximo de la apertura), NSW: número de vueltas de espira, SH: altura de la concha, SW: diámetro de la concha, UD: diámetro del ombligo, WBW: anchura de la vuelta del cuerpo.*

Specimen	NSW	SW	SH	UD	WBW	AW	AH	Keel
THC-01	5.00	18.47	10.62	0	12.41	9.3	6.3	YES: very marked
THC-02	4.90	19.43	10.61	0	12.66	9.3	6.2	YES: very marked
THC-03	4.80	20.55	10.61	0	12.90	10.4	7.0	YES: very marked
THC-04	4.80	20.17	10.11	0	12.45	10.6	6.7	YES: very marked
THC-05	4.85	17.32	9.91	0	12.02	8.9	5.8	YES: very marked
THC-06	5.10	18.39	10.55	0	12.75	9.3	6.2	YES: 1/3 of body whorl
THC-07	4.80	19.48	10.90	0	12.43	9.8	7.2	YES: very marked
THC-08	5.00	20.82	10.45	0	13.47	10.7	7.1	YES: very marked
THC-09	5.00	19.18	10.48	0	12.87	9.3	6.7	YES: very marked
THC-10	4.85	19.80	10.64	0	12.88	9.7	6.6	YES: very marked
THC-11	4.75	19.00	9.67	0	11.50	9.8	6.1	YES: very marked
THC-12	4.90	19.13	10.26	0	12.17	9.2	6.5	YES: very marked
THC-13	4.75	20.35	10.44	0	12.36	10.0	6.8	YES: very marked
THC-14	4.75	18.62	9.31	0	11.56	9.6	6.1	YES: very marked
THC-15	4.50	16.75	8.83	0	10.90	8.4	5.6	YES: very marked
THC-16	4.80	19.58	10.37	0	13.06	9.8	7.1	YES: very marked
THC-17	4.75	19.19	10.61	0	12.55	9.5	6.5	YES: very marked
THC-18	5.00	19.67	10.54	0	12.81	10.0	6.7	YES: very marked
THC-19	5.15	18.78	11.42	0	12.60	9.6	6.8	YES: mainly 1/4 of body whorl
THC-20	5.00	18.78	9.86	0	11.65	9.8	6.1	YES: very marked
THC-21	5.00	19.99	10.88	0	13.34	9.2	6.5	YES: very marked
THC-22	4.80	19.07	10.06	0	12.09	9.4	6.2	YES: very marked
THC-23	5.00	19.24	10.34	0	12.25	9.7	7.0	YES: very marked
THC-24	4.80	18.12	9.36	0	11.30	9.2	6.0	YES: very marked
THC-25	4.80	18.89	10.00	0	11.56	9.6	6.3	YES: very marked
THC-26	4.75	18.78	9.86	0	12.07	9.8	6.5	YES: very marked
THC-27	4.60	17.87	9.47	0	11.34	8.9	6.1	YES: very marked
THC-29	5.00	19.03	10.38	0	12.60	9.7	6.5	YES: very marked
THC-30	4.50	18.34	9.90	0	11.17	9.6	6.6	YES: very marked
THA-01	4.90	19.50	10.43	0	12.13	10.0	6.0	YES: very marked
THA-02	5.10	18.17	10.97	0	12.47	8.5	5.3	YES: marked in first 1/2 of body whorl
THA-03	4.85	18.64	10.57	0	12.23	9.4	5.2	YES: very marked
THA-04	4.90	17.74	10.06	0	12.11	9.0	4.9	YES: very marked
THA-05	5.00	18.42	10.32	0	12.59	9.2	5.1	YES: marked in first 3/4 of body whorl
THA-06	4.50	19.24	10.63	0	11.94	9.8	5.9	YES: marked in first 3/4 of body whorl
THA-07	4.75	18.29	10.81	0	12.52	9.6	5.4	YES: marked in first 1/5 of body whorl
THA-08	4.75	17.82	10.75	0	11.97	9.0	4.5	YES: very marked
THA-09	5.10	19.75	11.87	0	13.93	10.3	5.7	YES: marked in first 1/5 of body whorl
THA-10	5.00	18.44	10.57	0	12.78			YES: marked in first 1/4 of body whorl

Specimen	NSW	SW	SH	UD	WBW	AW	AH	Keel
THA-11	5.00	17.89	10.33	0	12.15	8.5	5.1	YES: very marked
THA-12	5.15	19.29	11.95	0	13.42	9.7	5.4	YES: marked in first 1/7 of body whorl
THA-13	4.66	16.90	10.93	0	12.30			YES: very marked
THA-14	4.50	17.55	9.69	0	11.33	8.7	5.7	YES: very marked
THA-15	4.66	16.82	10.26	0	10.88	8.5	6.2	YES: very marked
THA-16	5.00	17.54	10.60	0	12.18			YES: marked in first 1/3 of body whorl
THA-17	4.75	17.82	10.96	0	12.34			YES: marked in first 1/5 body whorl
THA-18	4.90	18.17	10.86	0	12.19	9.4	4.7	YES: marked in first 1/3 body whorl
THA-19	4.90	18.71	10.90	0	12.71	9.2	5.6	YES: very marked
THA-20	4.75	16.85	10.48	0	11.29	8.5	6.2	YES: marked in first 3/4 of body whorl
THA-21	5.00	18.04	11.43	0	13.02	9.4	5.3	YES: marked in first 1/4 of body whorl
THA-22	5.15	16.86	10.18	0	11.22	8.3	4.3	YES: marked in first 3/4 of body whorl
THA-23	5.10	17.39	11.40	0	12.44			YES: marked in first 1/2 of body whorl
THA-24	4.50	17.49	9.59	0	11.45	8.6	5.1	YES: very marked
THA-25	4.75	17.34	10.47	0	12.07	8.6	5.4	YES: marked in first 1/2 of body whorl
THA-26	4.80	18.62	10.68	0	12.87	9.0	5.1	YES: marked in first 1/3 of body whorl
THA-27	4.80	16.54	10.70	0	11.55	8.3	5.3	YES: marked in first 1/4 of body whorl
THA-28	4.50	16.65	10.07	0	10.80	9.1	5.2	YES: marked in first 4/5 of body whorl
THA-29	4.75	17.32	10.31	0	11.88	8.3	5.1	YES: marked in first 3/4 of body whorl
THA-30	4.50	19.69	10.30	0	12.39			YES: very marked
TPM-01	5.00	15.67	11.38	1.2	10.73	8.1	7.0	YES: only 1/3 of body whorl
TPM-02	4.90	15.78	11.35	1.2	10.53	7.9	7.3	YES: only 1/3 of body whorl
TPM-03	4.75	15.5	11.06	1.1	10.14	8.1	7.3	YES: only 1/4 of body whorl
TPM-04	4.80	15.30	11.43	1.1	10.40	7.7	7.1	YES: only 1/4 of body whorl
TPM-05	5.00	15.74	11.84	1.2	10.25	7.9	7.1	NO
TPM-06	5.00	16.94	12.00	1.1	11.07	7.9	7.4	NO
TPM-07	5.00	16.01	12.02	1.1	10.98	8.2	7.7	YES: only 1/3 of body whorl
TPM-08	5.00	15.58	12.50	0.9	11.15	7.9	7.1	NO
TPM-09	5.25	16.36	12.60	1.0	11.00	8.0	6.7	NO
TPM-11	5.00	17.26	12.82	0.8	11.00	9.2	8.6	NO
TPM-12	4.90	15.54	13.27	1.2	10.48	7.8	7.6	NO
TPM-13	5.00	16.24	12.00	1.1	10.58	8.2	7.2	NO
TPM-13	5.00	17.12	13.39	1.2	11.42	8.5	8.2	YES: only 1/4 of body whorl
TPM-14	5.20	18.68	14.98	1.5	11.00	9.4	8.6	NO
TPM-15	4.66	14.58	10.33	1.1	10.00	7.5	6.7	YES: only 1/4 of body whorl
TPM-16	4.55	15.46	11.10	1.2	10.33	8.0	7.4	NO
TPM-17	4.75	16.62	12.55	1.2	11.03	8.4	7.8	YES: only 1/6 of body whorl
TPM-18	5.45	18.75	14.30	1.3	11.92	9.1	8.5	NO
TPM-19	5.00	17.05	12.94	1.0	12.14	8.8	8.4	YES: only 1/3 of body whorl
TPM-21	5.20	18.03	14.94	1.3	11.95	9.2	9.0	NO
TPM-22	4.50	14.85	10.56	1.0	9.56	7.4	6.8	YES: only 1/4 of body whorl
TPM-23	5.00	16.13	11.87	1.2	10.94	8.0	7.2	NO
TPM-24	5.00	15.94	11.88	1.4	10.87	8.0	7.7	NO
TPM-25	5.00	16.49	11.89	1.6	11.44	8.1	7.2	NO
TPM-26	4.50	13.83	11.11	0.8	9.43	7.4	6.0	NO
TPM-27	4.30	14.76	10.59	0.9	9.37	7.5	7.0	YES: only 1/3 of body whorl
TPM-28	4.75	15.24	10.59	1.0	10.02	7.7	7.3	NO
TPM-29	4.30	14.10	10.27	1.2	8.85	7.3	7.1	NO
TPM-30	5.15	16.23	12.43	1.1	10.92	8.3	7.2	NO